ISSN 0704-3716

Canadian Translation of Fisheries and Aquatic Sciences

No. 5578

Evolution of the parasitic fauna of fish in the lakes of the Karelian-Kola limnological region (in connection with the typology of lake ecosystems)

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Original title: Evolyutsiya fauny parazitov ryb v ozyorakh Karelo-Kol'skoi limnologicheskoi oblasti (v svyazi s tipologiyei ozernykh ekosistem)

In: Parazitologiya/[Parasitology] 25(6): 527-535, 1991

Original language: Russian

Available from:
Canada Institute for Scientific and Technical Information
National Research Council
Ottawa, Ontario, Canada K1A 0S2

1992

13 typescript pages

Secretary of State-Secrétariat d'Etat

MULTILINGUAL TRANSLATION DIRECTORATE—DIRECTION DE LA TRADUCTION MULTILINGUE

LIBRARY IDENTIFICATION SHEET—FICHE SIGNALETIQUE

Translation from: **Russian** into: **English**	Traduction de: en:
Author(s)/Auteur(s): **Ye.A. Rumyantsev**	
Title in English/Titre en Anglais **Evolution of the parasitic fauna of fish in the lakes of the Karelian-Kola limnological region (in connection with the typology of lake ecosystems)**	
Title in foreign language/Titre en langue étrangère: **Evolyutsiya fauny parazitov ryb v ozyorakh Karelo-Kol'skoi limnologicheskoi oblasti (v svyazi s tipologiyei ozernykh ekosistem)**	
Source reference/Référence en langue étrangère: **Parazitologiya (Parasitology)**	
Publisher/Editeur: **"Nauka" Publishers**	Place of publication/Lieu de publication: **St. Petersburg, Russia**
Year of publication/Année de publication: **1991**	Volume & Issue No./Volume et numéro: **v. 25, No. 6**
Page numbers in original: Numéros des pages dans l'original: **527-535**	Number of typed pages: Nombre de pages dactylographiées: **12**
Client department/Ministère-Client: **DFO**	Branch or division/Direction ou division: **Scientific Publications**
Originator/Demandeur: **Dr. David Marcogliese**	Date of request/Date de la demande: **November 19, 1992**
Request No./N° de la demande: **3850584**	Translator/Traducteur: **N. De.**

CANADA

Secretary of State—Secrétariat d'État

MULTILINGUAL TRANSLATION — DIRECTION DE LA TRADUCTION

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	D F O	Scientific Publications	Ottawa
Bureau No. / N° du Bureau	**Language / Langue**	**Translator / Traducteur**	
3850584	Russian	N. De.	

Parazitologiya (Parasitology), 1991, v. 25, No. 6, p. 527-535

UDC 576.89:597.5 (—924.16)

Evolution of the parasitic fauna of fish in the lakes of the Karelian-Kola limnological region (in connection with the typology of lake ecosystems)

by Ye.A. Rumyantsev

Some of the general aspects and mechanisms of formation of the parasitic fauna of fish are discussed in relation to the type and succession of the lake ecosystems with the Karelian-Kola limnological region used as an example. The main types of lakes are characterized with the parasitological data taken into account. A system of lake typology and evolution is presented.

This particular study uncovers some of the general aspects and mechanisms of formation of the parasitic fauna of fish depending on the type and succession of lake ecosystems. The main types of lakes are characterized to some extent with the parasitological data taken into account. A system of lake typology and evolution is presented for the Karelian-Kola limnological region. Analysis of the parasitic fauna was carried out by means of Nikolsky's method of "faunistic complexes" (1947) with the changes introduced in it later by a number of other authors (Yakovlev, 1964; Strelkov, Shul'man, 1971; Sychevskaya, 1976; Donets, 1979; Pugachev, 1984).

According to these amendments, the boreal lowland, Upper Tertiary and Pontocaspian faunistic complexes are viewed by us as ecological groups of the same boreal lowland complex. These groups have adapted in different ways to low temperatures, which has affected their area of distribution. Unlike Donets, we have not used the names given to them by Nikolsky. The first group, the

Palearctic group, was regarded as the boreal lowland complex by Nikolsky. The second group is the amphiboreal group (Upper Tertiary complex according to Nikolsky), and the third group is the Pontocaspian group (Nikolsky's Pontocaspian complex). This method of parasitological investigation was first used by Gusev (1955). We are using it for the first time to study all the parasitic fauna, not just individual systematic groups, and for different types of lakes of a comparatively large region (Rumyantsev, 1989).

As the lake fauna evolved, a significant change occurred in the ratio of the [organisms] representing the boreal piedmont, arctic freshwater and boreal lowland faunistic complexes. Their distribution and abundance, as well as their role in increasing the trophicity of the lakes from north to south are depicted in Fig. 1.

The ecologic-parasitological studies on fishes carried out in Karelia and other regions (Shul'man et al., 1974, etc.) have shown that their parasitic fauna is quite sensitive to all changes in the hydrologic and hydrobiological conditions of the lakes. This constitutes sufficient grounds for assuming that the relationship between the parasitic fauna and the type and development of the lake ecosystems is quite significant. In order to comprehend the tendencies of change that reflect the development of lakes, let us examine those of the Karelian-Kola limnological region, which are found at various levels of development.

In our study, we have used, with some modifications (taking parasitological data into account), a lake typology system which incorporates elements of a number of classifications, primarily Gerd's, and in our opinion reflects with greater accuracy the general trend of the successional process of lake ecosystems, at least with regard to their parasite systems. In the proposed classification of lakes, the specificity of the Karelian-Kola limnological region has been taken into account, and, because of this, some of its details may not apply to other limnological regions.

Developing Gerd's concept of the genetic relations and bionomic characteristics of certain groups of lakes (Gerd, 1947, 1949), the primitive oligotrophic (ultraoligotrophic) lakes are regarded as the initial type of the majority of them. Such lakes do not exist today, since all of them have undergone some degree of development. The primary oligotrophic lakes were characterized by the presence of exclusively cold-water and oxyphilous representatives of the boreal piedmont and arctic freshwater faunistic complexes which formed the main nucleus of the fauna, including fish and parasites. Even today, some of the lakes of the Kola

Peninsula are completely devoid of boreal lowland species of fauna, e.g. parasites specific to carps.

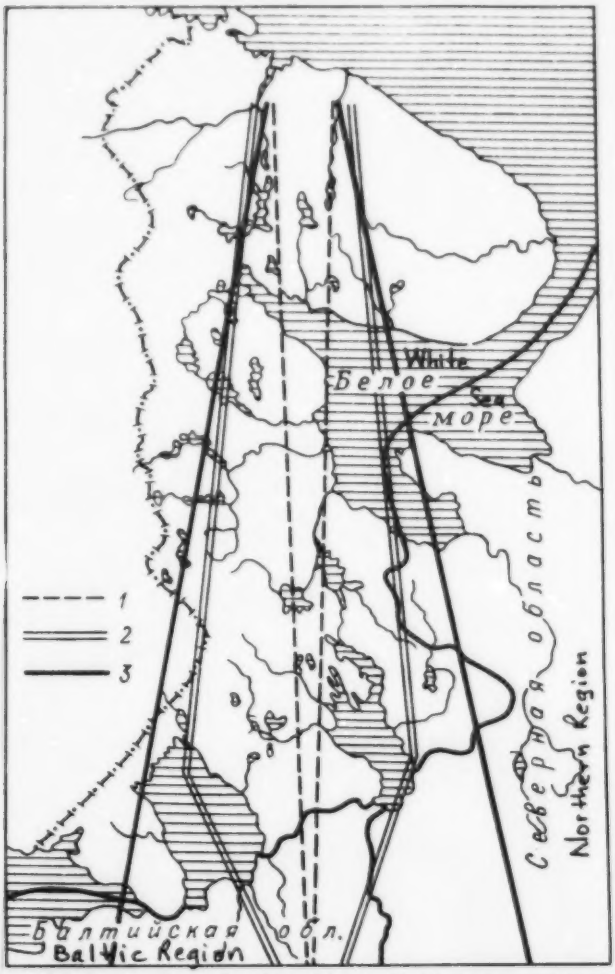

Fig. 1. Map depicting changes in the role played by individual faunistic complexes (1-3) in increasing the trophicity of lakes from north to south in the Karelian-Kola limnological region: 1 - boreal piedmont complex, 2 - artic freshwater complex, 3 - boreal lowland complex

Of the lakes in existence today, some of the Orthocladiinae lakes of the Kola Peninsula, which have undergone fewer changes because of their natural characteristics, are the closest to the primary oligotrophic lakes. These are predominantly subarctic oligotrophic lakes. The parasitic fauna in them is the youngest successionally, and is distinguished by the highest level of development of the boreal piedmont and arctic freshwater complexes among all the lakes studied. The boreal lowland complex plays a lesser role, and it is represented by the eurythermic palearctic group. Parasites specific to carps, which represent the boreal lowland complex, are not encountered (with the rare exceptions). The presence of

crustaceans of the genus *Salmincola* in the lakes is highly characteristic, and the relict leech *Acanthobdella peledina* is also encountered. The latter indicates that these lakes are very similar to the primary oligotrophic ones.

Gammaracanthus lakes, which include lakes Onega and Ladoga, are characterized by the highest diversity of parasitic fauna (over 200 species), the basis of which is formed by three well-developed faunistic complexes, namely the boreal piedmont complex, the arctic freshwater complex, and the boreal lowland complex which includes the Palearctic, Pontocaspian and amphiboreal groups. The heterogeneous nature of the fauna of these lakes is heightened also by the presence of species from some of the other complexes (brackish, Atlantic, Indian lowland). The presence of species such as *Myxidium salvelini*, *Gyrodactylus* sp. (*Salvelinus*), *Tetraonchus borealis*, *Salmincola salmoneus*, *S. thymalli* and *S. edvardsii* is highly characteristic of the parasitic fauna of Salmonidae. The large diversity of the fauna of these lakes is definitely determined by their large size and by the presence of numerous bays and inlets which provide a multitude of ecological niches. Gammaracanthus lakes, though similar to the initial type of primary oligotrophic ones, are nevertheless more different from the latter than the Orthocladiinae lakes of the Kola Peninsula. They already contain some significantly altered areas that have undergone some degree of eutrophication and dystrophication. Lakes Onega and Ladoga are characterized by active infiltration by representatives of the boreal lowland complex, including the Pontocaspian group, which had been forced back to the Caspian, Black Sea and Danube basins during the Glacial Period. They adapted mostly separate stretches of water and bays of these large bodies of water. Despite the fact that these changes were most significant and resulted in the formation of the most species abundant fauna of parasites as compared with other lakes, they were not so great as to exclude these bodies of water from the typically oligotrophic ones as a whole. Apparently, Lake Onega was such a typical ultraoligotrophic lake similar to the initial one (eutrophication and dystrophication delayed because of its large size) that, despite its being in the Baltic province of the Mediterranean subregion, it still contains many of the species of the boreal piedmont and arctic freshwater complexes. For example, a typical representative of the arctic freshwater fauna, *Acanthobdella peledina*, has been encountered in this body of water, at least at the beginning of the century.

The evolution of pontoporeid [????] lakes of the oligotrophic type was associated with the intensive development of glacial relict crustaceans. Their

mass development, especially Pontoporeus [???], provided the necessary conditions for the high abundance of those parasites with a life cycle in which relict crustaceans participate (*Metechinorhynchus salmonis, Cystidicola farionis*). Judging by the parasitological data, the pontoporeid lakes of the Konchezero group have, over the past decades, progressed considerably along the path of eutrophication. At the same time, the increase in the trophicity of the lakes (the food consumed in them by fish) was due more to the representatives of the arctic freshwater complex, namely organisms of the zoobenthos (relict crustaceans), than to the boreal lowland species. However, in some pontoporeid lakes (Konchezero), the process of eutrophication took place parallelly with others, i.e. dystrophication and humification. These processes and the faunistic changes associated with them proved to be so significant that they have allowed us to assign these lakes to another class, i.e. oligotrophic lakes in the process of eutro-dystrophication (located inside all three circles in Fig. 2).

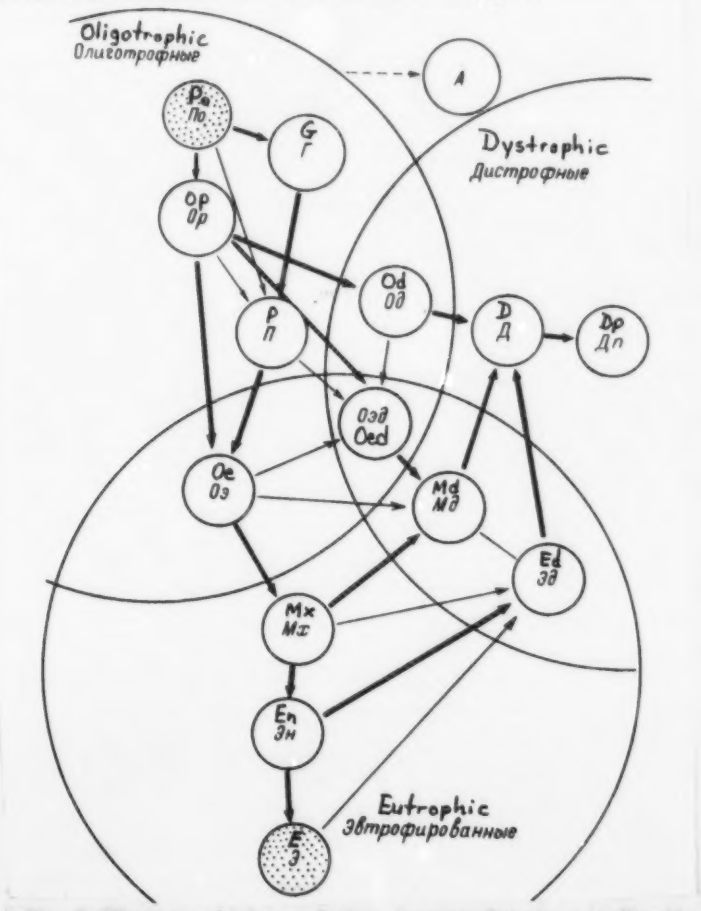

Fig. 2. Diagram of lake evolution (nomenclature as in Fig. 1)

Pontoporeid lakes preserve their oligotrophic nature up to a certain limit of eutrophication and change associated with this process, after which the fauna begins to undergo fundamental changes. The productivity of the relict crustaceans diminishes up to the point of their complete disappearance. Whitefishes also drop out, or, surviving for a certain period, diminish in abundance. The species of parasites associated with these hosts (relict crustaceans and whitefishes) disappear. Thus, the lakes pass into a new eutrophic state, in which the growth of trophicity takes place only by means of the boreal lowland faunistic complex, and is not associated with the arctic freshwater one. Therefore, in oligotrophic lakes of different classes, the role of individual faunistic complexes in increasing the trophicity of lakes differs from north to south in the Karelian-Kola limnological region.

Under the conditions of the Karelian-Kola limnological region, oligotrophic lakes, being exposed to humification by swamp waters, turn into dystrophied bodies of water more frequently and to a greater extent. The class of oligotrophic lakes in the process of dystrophication is located inside the two circles in Fig. 2. In these lakes, the development of processes associated with dystrophication predominates. Depauperization of the boreal piedmont complex of parasites occurs, for, since they are more rheophilous and oxyphilous, they do not tolerate any significant dystrophication. Such species as *Tetraonchus borealis, Dactylogyrus borealis, Gyrodactylus thymalli, G. nemachili, Proteocephalus thymalli, Cystidicoloides tennuissima* and *Salmincola thymalli* drop out. On the other hand, the depauperization of the arctic freshwater fauna is less pronounced, affecting not so much the species composition of the parasites, as the quanitative indices of host infestation. The glacial species associated with relict crustaceans undergo the most limited development. The progressive influx of swamp waters and the ferruginous formations on the lake bottom lead to a decrease in the biomass of zoobenthos. Many of the parasites with a life cycle in which benthic invertebrates participate become rare and dwindle to nothing. With the overall depauperization of zooplankton that occurs in these lakes, the relative significance of copepods in the diet of fish (primarily plankton-eaters) increases significantly. As a result, the conditions become more conducive to the proliferation of parasites with a life cycle associated with zooplankton. Representatives of the brackish and Atlantic complexes are not encountered.

On the whole, lakes of the oligotrophic type are characterized by the greatest diversity of faunistic complexes of parasites and narrowly specific species in them;

they ensure the necessary conditions for maximum specific and structural development of the fauna, and create the potentials for the formation of the highest number of trophic relations and the existence of parasites with different and complex life cycles. These developmental characteristics of the fauna of oligotrophic lakes are determined by autogenic processes which enable them to remain in a state of prolonged homeostasis typical of stabilized ecosystems.

The natural course of development of oligotrophic lakes, which is related to their eutrophication, as well as the rate and extent of the latter, depend on the temperature factor and are more pronounced in small bodies of water. This is why the number of eutrophic lakes increases sharply southward, and the eutrophication process itself becomes evident first of all in small lakes that warm up. The transition of oligotrophic lakes to eutrophic ones causes a decrease in the species diversity of the parasites, i.e. qualitative depauperization of the fauna occurs. Not only boreal piedmont species, but also many of the arctic freshwater ones drop out. For example, the complete absence of parasites with a life cycle involving relict crustaceans is one of the characteristics of all eutrophic lakes, beginning with mesotrophic ones. We have in mind species such as *Metechinorhynchus salmonis, Cystidicola farionis, Pseudoechinorhynchus borealis* and *Cyathocephalus truncatus*. Of the parasites with a direct cycle of development, crustaceans of the genus *Salmincola* are typically absent. Representatives of the brackish complex are also absent. Of the arctic freshwater species, only a few of the ones that are more resistant to eutrophication and found largely in whitefishes (*Ichthyocotylurus erraticus, Phyllodistomum conostomum, Argulus coregoni, Diphyllobothrium dendriticum, Triaenophorus crassus, Proteocephalus exiguus*) are still encountered.

At the same time, the process of eutrophication is accompanied by a growth in the numbers of some species and groups, namely infusorians (*Apiosoma, Trichodina*), trematodes (*Diplostomum*), and crustaceans (*Ergasilus sieboldi*). The life cycles of parasites with intermediate hosts that are water sowbugs (*Acanthocephalus lucii*) and pisidium (*Bunodera luciopercae, Allocreadium isoporum*) occur with success.

In the course of eutrophication, the composition of the dominant species of parasites changes. The representatives of the boreal piedmont and arctic freshwater complexes are replaced by Palearctic and Pontocaspian species of the boreal lowland complex. The diversity of parasites always diminishes, while their abundance does not always increase. In lakes with a diverse zooplankton, the infesta-

tion of fish with parasites associated with planktonic crustaceans is significantly lower than in lakes with a more depauperate zooplankton. This is due to the fact that the majority of plankton-eating fishes, which manifest feeding selectivity, prefer larger, slower-moving and schooled cladocerans to copepods. Therefore, these crustaceans, being fine filter-feeders, cannot serve as intermediate hosts for the majority of fish helminths (Shulman's paradox). The eutrophication of lakes is accompanied by a decrease in the diversity of parasites, an increase in the role of one faunistic complex (the boreal lowland complex), and by simplification of the trophic relations of the hosts and the life cycles of the parasites, which is a reflection of the overall weakening of the regulatory potentials of lake ecosystems of the eutrophic type.

Developing along the line of specialization in different directions, eutrophic lakes have a dissimilar parasitic fauna of fish, which is determined not so much by the qualitative compositiion of the hydrobionts (hosts), as by the feeding potentials that form between them. The changes occurring in the lakes are accompanied by the formation of conditions favorable for the more eurybiontic species of the boreal lowland complex. At the same time, the optimal conditions of some groups of animals are not the optimal ones for others, specifically the representatives of the cold-water fauntistic complexes. As a result, the latter decline in numbers, and finally disappear. This gives way to a different trend in the development of lakes undergoing eutrophication.

Mesotrophic lakes, despite the substantial diversity and development of various groups of parasites, still lose many of the species belonging to the boreal piedmont and arctic freshwater faunistic complexes. Mesotrophic lakes undergoing dystrophication, which have come a long way in the direction of dystrophication, are distinguished by comparatively low quantitative indices of fish infestation. As for the most eutrophic lakes, which are encountered in the southern part of Karelia, it can be said that the parasitic fauna in them have a smaller species diversity than mesotrophic lakes, mostly because of the dropping out of boreal piedmont and the majority of arctic freshwater species. At the same time, some representatives of the boreal lowland complex can attain a comparatively high abundance. The main difference between mesotrophic lakes as eutrophic bodies of water and oligotrophic lakes is said to be the extreme depauperization of the boreal piedmont fauna occurring in the lakes of the first type. Because of the greater oxyphyly and especially rheophyly of this complex, the conditions in mesotrophic lakes, even ones as large as Syamozero, prove to be unfavorable for

the development of its representatives. We do not regard mesotrophic lakes as an independent type, since they eventually become transitional ones, and it is impossible to draw a distinct boundary between the mesotrophic and the more eutrophic lakes. They should be regarded as the first stage in the development of eutrophic lakes in which the process of eutrophication is the least pronounced.

The effect of dystrophication is apparent not only in oligotrophic lakes, but also in lakes of the eutrophic type. The main difference between oligotrophic and eutrophic lakes in the process of dystrophication on the one hand and lakes of the dystrophic type on the other lies in the fact that the first, though greatly affected by dystrophication, are not affected to such an extent as to change from the initial type to a qualitatively new one. Gradually, lakes of the oligotrophic and eutrophic types undergoing progressive dystrophication become farther removed from their initial status and trend of development (along the path of eutrophication); they lose a number of ecological niches and the species diversity of the parasitic fauna, and finally diverge from their initial type to such an extent that they become a new dystrophic type.

Lakes of the dystrophic type include two classes, dystrophied lakes and strictly dystrophic lakes. Salonyarvi is an example of a dystrophied lake. It has diverged from its mesotrophic status to such an extent that we now regard it as dystrophic.

In our opinion, the main differences between dystrophied lakes and strictly dystrophic ones boil down to the fact that these lakes are usually comparatively large ones, with a more abundant fauna, including the parasities of fish (with some representatives of the arctic freshwater complex still encountered), and display an affiliation with the initial type of lakes from which they originated.

Lakes of the dystrophic type develop under the effect of allogenic processes, i.e. as if in reverse direction to the oligotrophic lakes. The extreme manifestation of this regressive succession is the dystrophic polyhumous type of ecosystem, which forms in small lakes with a monospecific carp ichthyocoenosis, and is characterized by relative instability, a sharp decrease in the specicies diversity of the fauna, including parasites, a decline in their numbers, and by the presence of only the boreal lowland faunistic complex.

Lakes known under the name of acidotrophic, or acidic, drop out of our diagram illustrating the evolution of lakes (Fig. 2). The specific conditions that emerge in these lakes, i.e. comparatively small dimensions, stagnancy, exceptionally weak mineralization and the absence of biogenic influx eliminate the

possibility of a natural increase in trophicity. The fauna, including parasites, is extremely depauperate. Basically, acidotrophic lakes do not develop in a specific direction, and differ significantly from dystrophic lakes, primarily in the fact that their low trophicity is the result of their initial status. This is why these lakes have been placed outside the circles in the diagram, i.e. they are singled out as an independent type which is not directly related to other types of lakes. Active and constant human intervention in these lakes (treatment with lime and mineral fertilizers, etc.) can bring about artificial, though probably temporary eutrophication.

Main types of lakes

Type	Class	Arbitrary acronym
Oligotrophic	1.1. Primary oligotrophic	Po
	1.2. Oligotrophic (without pronounced eutrophication and dystrophication)	O
	1.2.1. Orthocladiinae	Or
	1.2.2. Gammaracanthus	G
	1.2.3. Pontoporeid	P
	1.3. Oligotrophic in the process of eutrophication	Oe
	1.4. Oligotrophic in the process of dystrophication	Od
	1.4.1. Oligochaetous	
	1.5. Oligotrophic in the process of eutrodystrophication	Oed
Eutrophic	2.1. Mesotrophic (without pronounced dystrophication)	Mx
	2.1.1. Chironomus	
	2.2. Mesotrophic in the process of dystrophication	Md
	2.3. Eutrophic to the greatest extent (without pronounced dystrophication)	En
	2.4. Eutrophic in the process of dystrophication	Ed
	2.4.1. Chaoborine	
	2.5. Eutrophic	E
Dystrophic	3.1. Dystrophied	D
	3.2. Dystrophic	Dp
	3.2.1. Carp (polyhumous lambdae)	
Acidotrophic	4. Acidotrophic	A

Note: Lakes of the dystrophic type and lakes in the process of dystrophication (based on the degree of humification) are subdivided into oligohumous, mesohumous and polyhumous lakes.

In our opinion, the evolution of the main types of lakes proceeded in the following way. Primary oligotrophic lakes served as the initial type for all lakes. From them came Orthocladiinae lakes which are comparatively numerous on the Kola Peninsula and are the closest to oligotrophic lakes. Orthocladiinae lakes

developed in three directions. The first of these was related to the process of lake eutrophication. Smaller lakes located farther south were affected by this process first. They evolved into the eutrophic type of lake, the initial stage of which is the mesotrophic lake. The second direction of development was related to the process of dystrophication. Those Orthocladiinae lakes in which the processes of dystrophication by swamp waters and mineralization predominated from the very beginning became oligotrophic lakes undergoing dystrophication, and the latter became lakes of the dystrophic type. The third direction in the evolution of Orthocladiinae lakes led to oligotrophic lakes undergoing eutrodystrophication. These developed under the effect of two simultaneous processes, eutrophication and dystrophication.

The specific nature of the Karelian-Kola limnological region, which is related to low temperatures and an abundance of humic waters, has resulted in conditions which are not conducive to the completion of the eutrophication process as in the more southern areas. Furthermore, in some cases, there is a possibility of earlier transition to dystrophication of a lake, regardless of its trophicity. Generally speaking, the following three directions are noted in lake development: 1) the "traditional" path of eutrophication with subsequent dystrophication; 2) a direct transition from oligotrophic to dystrophic; 3) development by two simultaneous processes, eutrophication and dystrophication.

Therefore, the changes in the parasitic fauna described above show that, like all hydrofauna, it is unstable, changing and developing in complete unison with the body of water containing it. These changes are reflected in the diagram of lake development in the the Karelian-Kola limnological region. On the basis of this diagram, we have compiled a table which reflects the typology of the lakes and the causal-temporal relationship of individual types and classes. When compiling the diagrams and tables, we took into account the views of hydrobiologists in correlation with the results of parasitological research. The typology of lakes is, in the end, a reflection of the various stages of their evolution.

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